Assessing the Relation between the Spatiotemporal Microhabitat Heterogeneity and the Dispersion Patterns of Two Syntopic Small Mammals in a Midlatitude Temperate Forest

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Abstract

One of the basics problems in ecology is to understand the factors that shape the spatial patterns in the distribution of the species and the coexistence of close relatives species. Among the most critical factors governing the distributions and the coexistence of species are the spatiotemporal changes occurring in the microhabitat heterogeneity. Here, we assessed the heterogeneity of microhabitats and how they affect the spatial segregation of two species of small mammals (*i. e.*, *Peromyscus difficilis* and *P. melanotis*), which coexist in a temperate, mixed forest. We evaluated the microhabitat heterogeneity through multivariate statistics, using onto 23 habitat variables describing horizontal-vertical habitat structure along pluvial seasons. To detect specific microdistribution changes and habitat preferences by two species of small mammals, we used second-order spatial statistics and general linear models. According to their respective morphology and locomotive adaptations, the middle sized, midscansorial *P. difficilis* was resident all year long and preferred microhabitats with a high log ground cover, while the opportunistic, small sized, cursorial *P. melanotis* changed its occupancy area, depending on the density of herbaceous and woody plants cover. Under the more benign microhabitat conditions of the rainy season (denser plant coverage, milder temperature), both species showed closer microdistribution patterns; while these became repulsive at the less favorable conditions of the dry season (scarcer plant cover, colder temperature). Thus, we could confirm that seasonal changes of microhabitat heterogeneity promoted *Peromyscus* coexistence, through dispersion patterns reflecting partition of microhabitat resources.

Key words: Microhabitat selection, Use of space, Small mammals, Dispersion, Resource partition.

Introduction

Spatiotemporal habitat heterogeneity has a strong impact on coexistence among species since they become spatially segregated, according to niche preferences such as resource requirements (Valladares *et al.* 2015). Model simulations reveal the potentially important role of spatial heterogeneity and its complex and delicate interplay with dispersal in mediating long-term outcomes of species coexistence (Schreiber and Killingback 2013; Valladares *et al.* 2015). For example, an increase in the number of habitat types, resources, and structural complexity should increase the available niche space and thus allow more species to coexist (Currie 1991). Equally crucial for the maintenance of coexistence is the heterogeneity in time, with an influence on natural communities also variable depending upon the temporal scales (Valladares *et al.* 2015). Temporal fluctuations on habitat structure can stabilize coexistence via storage effect (Chesson 2000), when inter-annual variation in climate or resource availability favors alternatively one group of species over the others (Zavaleta *et al*. 2003). For instance, *Peromyscus* mice have been shown to respond to spatiotemporal habitat heterogeneity regarding species coexistence (M'Closkey and Fieldwick 1975; M'Closkey and Lajoie 1975), spatial segregation (Monamy and Fox 1999), and competition (Morris 1984; Seagle 1985).

Heterogeneous habitats contain patches of varying size, distribution, resources, environmental conditions, and species composition (Fahrig and Merriam 1994) that vary spatiotemporally, depending on observation scale and habitat type under study (Wiens 2000). It is highly likely that small size species such as small mammals perceive spatial habitat heterogeneity at a fine scale (microhabitat). Therefore, both movement and foraging by these kinds of mammals are affected by habitat heterogeneity (Bowne *et al.* 1999), having different responses among species or demographic groups within them

(Dooley and Bowers 1996). Here we focus on whether small mammals are capable of perceiving and to respond to spatiotemporal microhabitat heterogeneity.

Small mammals use resources selectively, based on their requirements for growth, survival, and reproduction, (Johnson and Gaines 1980). Several studies have quantified variation in resource use in heterogeneous environments either among congeneric and co-family mice species within a community (Kaufman and Kaufman 1989 and references therein). Indeed, syntopic related species are especially valuable for studies of spatial and resource partitioning, since they are most likely to be current or past competitors (Kalcounis-Rüppell and Millar 2002). Since habitat use varies spatiotemporally (Haim and Rozenfeld 1993) due to distribution and availability of resources, we expect that such variation also affects the use of resources and relationships among non-closely related species. In this study, the primary objective is to analyze how heterogeneity of microhabitats is structured and change through pluvial seasons in a temperate, mixed forest, and how such changes affect the coexistence of two syntopic species of *Peromyscus* (*i. e.*, *P. difficilis* and *P. melanotis*). Therefore, 1) We assess the presence of the spatiotemporal heterogeneity at a fine scale (microhabitat) according to vertical and horizontal structure indicators. 2) We evaluate the ecological dispersion patterns of two species of *Peromyscus*, and is tested if the use of space of the two small mammals is affected by the spatiotemporal changes in microhabitat heterogeneity. 3) We determine what kind of spatial relationships occur between both species, depending on seasonal changes in microhabitats heterogeneity (*i. e.*, attraction or positive: sharing of same microhabitats and resources; repulsion or negative: not sharing). Finally, we assessed which specific structural elements of each one of the microhabitats better explain the capture frequency of the two *Peromyscus* species between seasons.

Material and methods

Ethics statement

Animal capture and handling followed guidelines of the American Society of Mammalogists (Sikes *et al.* 2011). If animals died, corpses were prepared as voucher specimens to house them at the Mammal Collection of the Universidad Autónoma Metropolitana-Iztapalapa (UAMI, Ramírez-Pulido *et al*. 1989). Collecting permit, SEMARNAT-08-049-B, was issued by DGVS, SGPA-09712/13, SEMARNAT, to Alondra Castro-Campillo (ACC).

Study area

The study area was located in a temperate forest of conifers and broad-leaved trees at Parque Nacional Desierto de los Leones (PNDL, CONANP 2006), Mexico City, within the Transmexican Neovolcanic Range. Temperature averages 12.6 ± 6 °C from April to July, while it descends to 8.1 ± 2 °C from December to February. Rainfalls occur from late spring throughout summer (May to August), with average precipitation of 235 ± 30 mm, though this period can go until mid-fall (October). From winter to early spring (December to March), precipitation average becomes 12 ± 4 mm, introducing a dry and cold climate (PNDL, CONANP 2006). Dominating vegetation by strata includes canopy, *Abies religiosa, Pinus hartwegii, P. leiophylla, P. montezumae, Prunus serotina, Garrya laurifolia, Salix paradoxa, and Buddleia cordata; understory shrubs, Baccharis conferta* and *Senecio spp.,* and herbs, *Acaena elongata, Sigesbeckia jorullensis,* and *Alchemilla procumbens*; ground level, a rich variety of mosses and fungi.

Mice sampling

We captured mice along ten months (October 2013- August 2014), including the dry and wet seasons within a 2,475 m2 surface plot (Fig. 1) at 2289 m. The plot was gridded (12 vertical lines, A-L; 10 horizontal lines, 1-10) marking intersections each 5 m with buried wood stakes (150x2.5x2.5 cm) to construct a coordinate system for independent sampling stations, where we set 120 Sherman live traps (Tallahassee, FL 32303, USA), baited with oat flakes and vanilla scent (Fig. 1). Traps were set for two continues nights (2400 trap-nights), shortly before dusk, left open overnight, and checked at next day dawn. We recorded the frequency of captures of each of the two *Peromyscus* in the 120 sampling stations during all trapping sessions. All the traps were cleaned, and bedding was changed at each trap check event (Brouard 2015). All the traps were set randomly in each sampling station to avoid bias in frequency quantification due to recurrence behavior or shyness of the mice to the trapping. Coordinates of all trapped mice were recorded and the species and sex determined through visual inspection.

Microhabitat features

To assess spatiotemporal heterogeneity of microhabitat within the entire plot, we delimited an influence zone (sub-plot, Fig. 1; close-up, Fig. 1), drawing a rectangle of 2.5 m^2 around each sampling station. 23 variables were sampled (Table 1) once in each influence zone in both seasons. The sampling of the entire plot took ten days, we sampled one transect per day, starting at 9 am in the second week of the most represented month

of rains (July) and in February for the dry season (PNDL, CONANP 2006). These variables have been proved to be components of the vertical and horizontal structure of the microhabitat. Also as factors affecting the distribution of small mammals at fine scales (Morris 1984, 1987; Stapp 1997; Jorgensen 2004, Coppeto *et al.* 2006; Villanueva-Hernández *et al.* 2017). Environmental variables include vegetation coverage at different heights (VC10-100 cm), number of herbaceous forms (FH11-15), and number of woody forms (VF21-25) at five different heights: 10, 25, 35, 50, and 100 cm, respectively. Rock coverage (RC), logs coverage which include stumps and fallen trunks (CLO); coverage of organic matter (OM); coverage of bare soil (BS); vegetation species richness (VR); total herbaceous plants (TH); total woody plants (TW) and the number of burrows (BW) also were sampled (Table 1). Overall, these variables provide information about possible refuges for the small mammals against predators, some elements of microhabitat also imply spaces for resting, breeding, for food resources and safe roads to move from one place to another, avoiding predation risk (Jorgensen 2004). Detailed information about ecological meanings for each variable appears in Table 1.

We adapted Canfield's (1941) method of Line Intercept (LI) to measure all variables in each pluvial station, for it allows sampling within-plot variation and quantifies changes, both in plant species cover and height over time, by using transects located within a plot. We drew eight graduated transects (cm) from the respective influence zone of each station to cover the 2.5 m^2 sub-plots (Fig. 1); four 2.5 m transects were cardinally oriented (N, S, E, W), while other four 3.30 m ones were diagonally oriented (NE, NW, SE, SW). Only plants intercepted by diagonal transects were counted for vegetation species richness, number of life forms at different heights (herbaceous and woody plants), and total herbaceous and woody plants; while all transects were used to measure plant coverage at different heights, as well as coverage of fixed elements (*i. e.*,

rocks, logs, bare soil, dead organic matter). We calculated coverage percentage of each variable within the sub-plots with the formula $\sum(Xi)\frac{100}{2400}$, where Xi is centimeters occupied by every plant in each transect, and 2400 equals total longitude (sum of the eight transects). We counted the number of woody and herbaceous plant life forms at different heights and burrows within each influence zone of every sampling station. We took each hole in the ground ca. 8-12 cm of diameter as a potential burrow for both *Peromyscus* (Álvarez-Castañeda 2005; Fernandez *et al.* 2010).

Statistical data analysis

We standardized all variables and run statistical tests at $p \leq 0.05$. We did not found multicollinearity among the 23 variables which was assessed by examining the Variance Inflation Factor (*i. e.,* all values were in a threshold <6) (Zar 1999). To identify and categorized microhabitat heterogeneity within the grid, we performed two independent Hierarchical Cluster Analysis (HCA) in JMP® (ver. 9, SAS Institute Inc., Cary, NC, 1989-2007) for each season. These analyses allowed us to cluster the sample stations with similar characteristics according to with the sampled variables for both seasons. We used Ward´s method (1963) where the distance between two clusters is the ANOVA' sum of squares between them, added up over all variables. Visual inspection of the dendrogram and no drastic changes in the variance screeplot, gave us three general groups of stations for both seasons, which we interpreted as distinct microhabitat types (M1-3). We further statistically validated such microhabitats carrying out independent Discriminant Analyses for both seasons (DA, Addinsoft SARL's XLSTAT 2013; F = 9.99 dry; F = 9.64, rains; Wilk's Lambda = 0.0001 in both) (Fig. A.1). These analyses allow us to know what type

of microhabitat corresponded to each sampling station. Thus, we constructed two different maps, assigning to each sampling station a color mark that represented the three different microhabitats for both seasons (M1: red, M2: green, M3: blue) (Fig. 2, Fig. A.1). To create typologies that describe at a fine scale the behavior of each one of the 23 variables within three microhabitats for both seasons, we built a plot whereas "Y" axis comprises of the 23 standardized variables and in the "X" axis corresponds to the three microhabitats constructed with the same 23 variables (Fig. A.1).

Due to not all 23 variables did not reveal a normal distribution, We applied two different tests to analyze the distribution changes on each microhabitat variable between the rainy and dry seasons. First, distribution normality was checked of every variable with Kolmogorov-Smirnov tests (Zar 1999). Thus, We used Student's t-parametric tests for variables normally distributed and non-parametric Wilcoxon test for non-normal variables (Table 2). To know whether the number of stations structuring each type of microhabitat changed between seasons (seasonal microhabitat heterogeneity), we used a contingency table and x^2 test. All these analyses were performed with XLSTAT 13 (Addinsoft SARL). To examine the association between changes in spatial heterogeneity of microhabitats and dispersion patterns of *Peromyscus*, along with the entire grid, we conducted a Contingency Tables Analysis. Then, for visualizing associations between the *Peromyscus* and microhabitats, we performed a Correspondence Analysis with the constructed Contingency Tables for both seasons, including the abundance of each species in the three microhabitats (Table A.2).

Spatial analysis

To map variations in point density captures of small mammals, and to find density gradients across the plot area, we used the Kernel function (PAST, ver. 3.14, Hammer *et al.* 2001). To test the ecological dispersion patterns of both species within the plot (*i. e.*, clustering or overdispersion) for both seasons, we used a "Nearest Neighbor Analysis" (Clark and Evans, 1954) using the PAST software (ver. 3.14, Hammer *et al.* 2001). We applied the Wrap-around edge effect adjustment which is only appropriate for rectangular domains as our plot sampling (Hammer *et al.* 2001). In general, the "Nearest Neighbor Analysis" compares the mean distance of each main individual from its nearest neighbor of the same species with the mean distance expected for a set of points randomly dispersed at the same density (Vázquez and Álvarez-Castañeda 2011). The ratio of the observed mean distance to the expected distance (R) indicates how the observed distribution deviates from random. Clustered points give $R<1$, Poisson patterns give $R\sim1$, while overdispersed points give $R>1$.

To assess whether both species were associated or disassociated, we compared dispersion patterns between the two mice, using Ripley's K bivariate function (Ripley 1977), since the method considers all distances among individuals located under a Cartesian scheme (X,Y) in a quadrat plot (Ripley 1976, Dale 1999, Zavala-Hurtado *et al.* 2000). We used PASSaGE (*ver. 2*, Rosenberg and Anderson 2011) to carry out Ripley's bivariate K analysis. We used the option to test the associations conditional on current locations hypothesis in PASSaGE. In this test, the point locations remain fixed, and only the types are randomized (the two *Peromyscus*). The number of each type remains fixed, but the association of each type with a specific, fixed location is randomized. In this case, one is not testing whether the points are themselves random or clustered, but rather

whether the association of type A with type A (*P. difficilis vs. P. diffiiclis*) (or *P. difficilis vs. P. melanotis*) is what one would expect given the locations of the points as fixed (Rosenberg and Anderson 2011). We assigned coordinates to each sampling stations considering 5 m distance between them. Therefore, because each sampling station had a Cartesian coordinate system, we used as data input each station were we capture mice. Thereby, our null hypothesis involved independence between our two species *P. difficilis* and *P. melanotis* (Ripley 1976, Diggle 1983, Dale 1999), since we were interested in whether points of a specific type (*P. difficilis*) were associated, or disassociated, with points of the other specific type (*P. melanotis*). In other words, Ripley's $K_{12}(d)$ allowed us to assess spatial attraction or repulsion between the two species, among the stations of the plot. To evaluate the statistical significance of $K_{12}(d)$, we estimated 95% confidence envelops (95% CI), using a Monte Carlo procedure, based on 1000 stochastic relocation simulations of the sampling stations in the plot (Upton and Fingleton 1985; Bailey and Gatrell 1995; Zavala-Hurtado *et al.* 2000). When L(*d*) was positive and took values over the upper limit of the confidence region, we inferred dissociation or repulsion between the *Peromyscus* at the corresponding (*d*) scale; whereas a significant negative deviation indicated us a pattern of association or attraction between the two mice (Dale 1999). If L(*d*) remains within the limits of the 95% CI for a given value of *d*, the null hypothesis of independence between the two contrasts cannot be rejected (Dale 1999). The height of the L(*d*) function (peak height) indicates the intensity of the association or repulsion. Control for edge effect was carried out for analysis by rescaling the counts based overlap with the study boundary setting the options area/volume which has been recommended for quadrats plots (Rosenberg and Anderson 2011).

Prediction of microhabitat elements affecting the use of space by each species

To determine which specific environmental variables best explained the frequency of both species at each season, we performed Generalized Linear Models (GLMs), using JMP® (ver. 9, SAS Institute Inc., 1989-2007, Cary, NC,). First, we conducted a Principal Component Analysis (PCA) onto the means of the 23 variables to obtain functions summarizing the most significant variance at each season. Because in both seasons the three first functions summarized a good portion of the variance (38.61 for the dry season and 45.92 for rains), we used these functions to construct the GLMs. Therefore, we assessed different models using the PCs as effect variables to explain the frequency of the individuals of both species for both seasons. Then, to visualize the fit of the model, the predicted values from the GLMs were plotting against the Principal Components of the best model chosen. For each species, the response variable in the models was the capture frequency at each trapping station of the grid, and we assumed a Poisson distribution with a log link function. Criteria for the selecting models that most explained the frequency of mice for each species at each season in the sampling stations included: model significance of $p < 0.05$; lowest Akaike Information Criterion (AIC), *i. e.,* a measure of variance explained by the model (Posada and Buckley 2004); Pearson goodness-of-fit ($p < 0.05$) and its deviation (Deviance; $p < 0.05$); as well as the biological and ecological meaning of results.

Results

The Behavior of 23 variables of microhabitat between seasons

When considering the mean value over all stations, 16 out of the 23 environmental variables showed a significant difference between the two seasons (Table 2, Fig. 3, Fig. A.1). The main changes were observed for variables related to herbaceous vegetation, according to plant coverage at different heights, and vegetation species richness (VR). As expected in overall, woody life forms were more stable between seasons (Table 2, Fi. 3, Fig. A.1). Components of microhabitat showing no statistical change between seasons were frequency of 10 cm height herbaceous plants (FH11), the frequency of both 35 cm (FW23) and 50 cm (FW24) woody plants, as well as coverage of logs (CLO), rocks (RC), and bare soil (BS). Therefore, space configuration given by these structural features remained stable in both seasons (Fig. 3).

Microhabitat heterogeneity

The dendrogram from cluster analysis revealed three different classes of microhabitats (M1, M2, and M3) within the sampling plot in each season (Fig. A.1). M1 included more sampling stations during the dry season, while M2 covered the majority of sampling stations during the rainy season (Fig. 2, Fig. A.1, Table A.1). Indeed, Fisher's exact test of Contingency Tables Analysis revealed significant changes in the number of sampling stations ($p = 0.004$) from dry to rainy seasons. The main changes occurred between M1 ($x^2 = 2.123$, $p < 0.05$) and M2 ($x^2 = 3.348$, $p < 0.05$), especially in the latter, since it augmented 24 sampling stations from the dry season to the rainy season (Fig. 2, Table

A.1). Conversely, the number of sampling stations remained quite stable in M3 (x^2 = 0.011) throughout the study (Fig. 2, Fig. A.1, Table A.1).

Discriminant analyses validated heterogeneity of the three microhabitats (Fig. 2) within and between pluvial seasons. the percentage of variance associated to each discriminant function was clearer during the rainy season (dry season: F1 = 58.67 %, F2 = 42.32 %; rainy season: F1 = 72.581 %, F2 = 27.419 %) (Fig. 2, Fig. A.1). Discriminant functions explained variation due to woody plants in the understory in the dry season, while herbaceous vegetation together with decayed matter and logs became more relevant at rains (Table A.3). Wilk's Lambda showed that at least the mean of one microhabitat differed statistically from the others either in the dry and rainy season (p = 0.0001; p = 0.0001, respectively) (Fig. A.1). These results corroborated spatial and temporal heterogeneity drawn from cluster analysis of individual station features in the grid plot. During the dry season, 93.33 % of individual sampling stations remained correctly classified, and 94.17 % of them during the rainy season (Fig. 2).

Description of microhabitats within the plot

Microhabitat 1. M1 (Fig. 2, Fig. A.1) was characterized by low amounts, or absence, of vegetation cover at different heights (VC) and by a low frequency of herbaceous and woody plants (FH and FW, respectively). In contrast, organic matter on the ground (OM) was the most frequent component. This microhabitat was also distinctive for having extensive coverage of logs (CLO) on the ground and for being the microhabitat with the significant presence of burrows (BW).

Microhabitat 2. M2 (Fig. 2, Fig. A.1) was the largest area covered by herbaceous life forms at different heights; vegetation species richness (VR) and the total number of

herbaceous plants (TH) also remained very high. Woody life forms at 25 cm (FW22) were present but at low frequencies, while FW24 and FW25 remained at higher frequencies. Coverage on the ground of small logs or dead wood (CLO), of rocks (RC), and organic matter (OM) were shallow during the study. Bare soil surface (BS) increased to higher amounts during the dry season, while it decreased during the rainy season. There were no burrows (BW) in this microhabitat.

Microhabitat 3. In M3 (Fig. 2, Fig. A.1), VC25, VC35, VC50, and VC100 showed high values, while vegetation species richness (VR) averaged the highest compared to other microhabitats. The total number of woody plants (TW) and frequency of woody plants at different heights (FW21-25) remained very high, while the total number of herbaceous plants (TH) was low. Vegetation coverage at 10 cm (VC10), rocks (RC), logs (CLO), and bare soil surface (BS) were low during the dry season; however, VC10 increased in the rainy season. Conversely, OM was present in the dry season but decreased in the rainy season. The number of burrows (BW) remained quite scarce.

Association between the microhabitats and species

Kernel Graphs (Fig. 4) indicated that the two species used space distinctivel, since they were differentially scattered along the plot. *Peromyscus difficilis* was more abundant during the dry season, occupying a large portion of the plot. Instead, *P. melanotis* increased its distribution during the rains when it seemed to displace *P. difficilis* into other sampling stations (Fig. 4). Distribution rearrangements between seasons implied that one species occupied some stations more frequently than the other, and vice versa (Fig. 4). Indeed, the two x^2 tests yielded statistical abundance differences in each species at both microhabitats and seasons (Table A.2: dry season; R^2 (U) = 0.09, n = 111, df = 2,

Likelihood Ratio x^2 = 15.07, p = 0.00005; rainy season; R^2 (U) = 0.02, n = 168, df = 2, Likelihood Ratio x^2 = 6.40, p = 0.0406).

During the dry season (Fig. 5 and Table A.2), *Peromyscus difficilis* was highly related to M2 (80 % captured mice) and frequently related to M1 (64 % captured mice); conversely, *P. melanotis* was captured more frequently in M3 (66 % captured mice). Spatial use of microhabitats changed for both species in the rains (Fig. 5 and Table A.2), showing a microhabitat partition again, though less visible: in the Correspondence Analysis, 61 % of mice caught in M1 were *P. difficilis*. This species was also related to M3, while 60% of mice caught of *P. melanotis* were captured in M2.

Spatial Patterns

The Nearest Neighbor Analysis revealed that in both seasons both species showed a significant clustered pattern within the plot (Table 3). In the dry season, the mean distance between individuals of *P. difficilis* displayed to be more clustered than the individuals of *P. melanotis*. However, the mean distance between individuals of *P. difficilis* increases in the rainy season, while individuals of *P. melanotis* showed a reduction in their area occupied (Table 3).

On the other hand, during the dry season, Ripley's bivariate K showed a statistically significant pattern of repulsion for both *Peromyscus* in almost all analyzed distances of the entire plot, excused at 2 m where it shows an attraction pattern (Fig. 6a). Such repulsion pattern turned over in almost all distances during the rainy season (Fig. 6b), since the two species became more associated, sharing microhabitats in almost all capture stations. However, during the rainy season, significant statistical peaks of repulsion reappeared between the species at distances of five, ten, and 14 m (Fig. 6b).

Analyses also revealed the intensity of these patterns; *e.g.*, the likelihood for finding individuals of *P. difficilis* and *P. melanotis* together at the same capture station was very low during the dry season (Fig. 6a), while this probability increased in the rainy season (Fig. 6b).

Structural components of microhabitats affecting the distribution of small mammals

During the dry season, PC1 and PC3 predicted the frequency of *P. difficilis* according to the best Generalized Linear Model for this season (AICc 212.55) (Table 5, Fig. 5c). Environmental variables with higher scores in the PC1 ($p = 0.0186$) were the total number of herbaceous plants (TH), vegetation species richness (VR), and vegetation cover at 10 cm height (VC10). In PC3 ($p = 0.0001$), characterizing variables were the number of logs on the ground (CLO), as well as the presence of burrows (BW) (Table 4, 5, Fig. 5c). These five variables were also the main elements characterizing M2 (PC1) and M3 (PC3), the two habitats where the frequency of capture of *P. difficils* was the higher. As for *P. melanotis* (Fig. 5c), the frequency of capture of *P. melanotis* was positively related to PC2 (AICc = 204.47, $p = 0.0001$). Here, among the four variables with higher scores, were the total number of woody vegetation (TW) and frequency of woody life forms characterizing 10 cm height (FW21), the two main elements at M3 for the dry season (Table 4, 5, Fig. 5c).

During the rainy season, a similar pattern of microhabitat partition occurred between the two species. The best GLM model for *P. difficilis* in this season was (Table 4, 5, Fig. 5c) was mainly associated with the total number of woody plants (TW), herbaceous forms at 50 cm (FH14), woody forms at 10 and 100 cm (FW21, FW25, respectively) and with the number of logs on the ground (CLO), in PC2; and with were

number of logs on the ground (CLO), and organic matter (OM) in PC3 (AICc = 286.76, $p = 0.0001$) (Table 4, 5). The latterly involved variables with a high presence at M1 (PC3) and M3 (PC2) during the wet season, where *P. difficilis* was more frequently captured. On the other hand, *P. melanotis* (Fig. 5c) was only associated to PC1 (AICc = 241.01, $p = 0.0343$). The primary variables characterizing this component were the number of total herbaceous plants (TH), vegetation species richness (VR), and the plant cover at almost all analyzed heights (VC10-100 cm) (Table 4). Therefore, results of Contingency Tables Analysis, Correspondence Analysis, and GLMs models showed that the two syntopic species of *Peromyscus* switched and split resources in space, as environmental conditions changed.

Discussion

Our findings on microhabitat relations of rodents in a patch of a mid-latitude temperate forest, concur with the habitat heterogeneity coexistence hypothesis (Cramer and Willig 2002; Valladares *et al.* 2015). We found that both *Peromyscus* were sensitive to slight changes in microhabitat structure and that the three microhabitats provided different resources for each one. Our results also suggest that coexistence between these syntopic *Peromyscus* is facilitated by temporal differences in space structure, and probably also by changes on the availability of both food and shelter that go with it (Pianka 1973; Schoener 1974). For instance, *P. difficilis* was more related to M1 and M2 by the dry season, while *P. melanotis* was highly related to M3. Conversely, *P. difficilis* was more related to M1 and slightly captured to M3 by the rainy season, while *P. melanotis* was highly related to M2. Partition in space use has already been documented for coexisting species of *Peromyscus* within a community; *i.e.*, extensive studies of niche partitioning by

Peromyscus leucopus and *P. maniculatus* (Kaufman and Kaufman 1989). Moreover, several studies have demonstrated variation in spatial resource use by congeneric species (Barry *et al.* 1990; Dooley and Dueser 1996; Kalcounis-Rüppell and Millar 2002).

In our study, *P. difficilis* remained related to M1 and M3 in both seasons, especially to the former during the wet season. The number of fallen logs was very high at M1, while understory complexity, together with woody vegetation, were more representative in M3. Such microhabitats represent small patches of food for small mammals, offering invertebrates (Bellows *et al.* 2001), flowers, grains, and fungi items (Bowman *et al.* 2001). In these microhabitats, individuals of *P. difficilis* can also use fallen logs as shelter, as well as pathways for quick and straight locomotion inside the forest (Bellows *et al*. 2001; Dewalt *et al.* 2003). Indeed, fallen logs promote structural complexity of forests and may enhance positive interaction among species of small mammals (Bowman and Facelli 2013). GLM's analyses showed that abundance of *P. difficilis* was explained by PC1 and PC3 during the dry season and by PC2-4 in the rainy season. In the dry season, variables contributing most to PCA ordination in PC1 and PC3 were the total number of herbaceous vegetation (TH) and the number of logs on the ground (CLO), as well as burrows (BW). While in the dry season, PC2-4 represented woody vegetation (TW), number of logs, burrows, and understory complexity (VR). Bellows *et al.* (2001) found a similar result in a high latitude temperate forest (Virginia, USA), where distribution of a small mammal, generalist species was associated with the diameter of fallen logs, the frequency of shrubs, and degree of canopy closure. Association between rodents and fallen logs was also documented for *Nectomys squamipes* that builds up its nests inside decomposed, fallen logs (Briani *et al.* 2004); this has also been recorded for other rodent species in several biomes with different vegetation types (*e. g.*, *Rattus rattus*, *Nesomys audeberti* in Lehtonen *et al.* 2001; *Oligoryzomys*

nigripes in Dalmagro and Vieira 2005). In contrast, *P. melanotis* showed a close relation with only one PC over each pluvial season. During the dry season, the frequency of this species was only related to PC2, which represented the total number of woody vegetation (TW). Then by the rainy season, the species became only related to PC1, which accounted for understory complexity dominated by herbaceous life forms (TH). Relationships between frequency of rodents and habitats with increased understory density has been interpreted as protection against aerial predators (Dalmagro and Vieira 2005), or as preference for more complex habitats that enable for vertical stratifications and, thus for extended coexistence inside fragments (Grelle 2003; Johnson 2007).

Intrinsic factors as sex and mating system must also be related to the coexistence of both *Peromyscus*. For instance, the Nearest Neighbor Analysis revealed that in both seasons both species showed a significant clustered pattern within the plot (Table x). However, the mean distance between individuals of *P. difficilis* displayed to be more clustered than the individuals of *P. melanotis* especially during the dry season. Indeed, the mean distance between individuals of *P. difficilis* increases in the rainy season, while individuals of *P. melanotis* showed a reduction in their area occupied (Table x). This patterns are related with the breeding season of both species. Our data (not published) revealed that during the dry season were captured more individuals with signs of reproductive activity (males: inguinal vs. scrotal testicles, females: alopecia, the presence of milk, the appearance of the vagina, gestation). While for *P. melanotis* occurs during the rainy season. Individuals need different resources requirements to fulfill the breeding season and this impact on its dispersion and coexistence. Likewise, the partition of space by these syntopic deermice must be facilitated by their respective locomotive habits as semiarboreal (*P. difficilis*) and cursorial (*P. melanotis*). The long tail of *P. difficilis*, must enable it to rush and climb along shrubs or trees (Álvarez-Castañeda 2005), thus easing

its preference for habitats where it can escape from predators. Indeed, adult color coat changed in *P. difficilis* between pluvial seasons, becoming more similar to ground litter; *e. g*., in this resident deermouse, color phenotype plasticity must be a cryptic response elicited against predators. On the other hand, a smaller sized body, together with a shorter tail and narrower soles (Fernandez *et al*. 2010), should enable the cursorial *P. melanotis* to occupy such zones as M2 and M3, where predators cannot easily spot it through a dense vegetation cover, so it can scape very quickly. Indeed, high shrubs cover provide both protection from predators and food sources, since seeds may be concentrated under shrub canopies (Thompson 1982; Mohammadi 2010). In fact, rodents usually avoid foraging in unsheltered microhabitats and forest edges where they are more likely to be spotted by avian (Kotler *et al*. 1991) and other vertebrate predators (Morris and Davidson 2000; Mohammadi 2010). In this study, we define to *P. melanotis* as an opportunistic species throughout the study area because the capture frequencies of the individuals only increased when the environmental conditions (*i. e.* availability of resources) became more beneficial for the survival of these. That is, throughout the time of capture except for the rainy season, its frequency of capture remained at low levels compared to those of *P. difficilis* (resident species), increasing drastically in the rainy season when there is greater accessibility for the use of resources and competition between the two species decreases. Therefore, *P. melanotis* generally showed a more opportunistic pattern of habitat occupation as compared to the larger sized *P. diffiilis*. Chupp (2002) also showed an opportunistic habitat by small-sized *Peromyscus leucopus*, which he related to predation risk. Further studies about the influence of predation on the opportunistic behavior of *P. melanotis* are needed.

One possible consequence of such extrinsic and intrinsic operating factors is that *P. difficilis* remained more abundant and always present at the microhabitats with more

stable elements in the study area (our unpublished data), while *P. melanotis* only increased its abundance during the rainy season, when environmental conditions became more benign, and plant cover became denser. Since rains promote an increase of primary productivity, allowing more resource availability (mainly food) and enhancing microhabitat carrying capacity, such habitat changes facilitate coexistence between both *Peromyscus*, and with other small land mammals in the area (Castro-Campillo *et al.* 2008, 2012). Ripley's bivariate K supported and shed light into such outcome since the species showed repulsion between them in almost all analyzed distances during the dry season; *i.e.*, due to resources availability are more scarce during this season, is almost null that a mixed pair of mice used the same microhabitat. Moreover, as in this season is the primary breeding season of *P. difficilis* is probably that territoriality behavior can occur. Conversely, the intensity of such repulsion decreased substantially during the rainy season; moreover, at some analyzed distances, the two deermice showed an association pattern. Holding our results that the increase of resources available during the rainy season can allow that the species can share the habitat. Thus, our results indicate that in these two syntopic *Peromyscus*, both microhabitat use and spatial organization are seasonally variable (Brown and Zeng 1989; Cramer and Willig 2002).

Finally, we want to highlight and recommend our sampling of environmental features and quantitative analyses, especially for Ripley's bivariate K, as neither one has been extensively used in studies focusing on the spatial dynamics of dispersion in small rodents, despite its important advantages. The methodological approach used here, together with the gathered evidence became relevant for providing us with necessary information about the ability of this two *Peromyscus* to split resources in a mid-latitude temperate forest at the edge of a megalopolis, which continuous growth produces fragmentation and patching of natural microhabitats. Therefore, our local scope was

explicitly designed at this initial point, to focus on small-sized rodents with low vagility. Besides, we successfully aimed to reconstruct vegetation structure, to provide us with clues as to how to eventually manage such perturbed ecosystems for conservation purposes. We also think that our methodology can be helpful in other scenarios for understanding small rodents, such as ethological dynamics, activity patterns, and reproductive systems at either or both intra or interpopulation levels.

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Table 1. Environmental variables used to measure the horizontal and vertical structure of microhabitat at each sampling station, showing its ecological interpretation (kind or resource type) for both species of *Peromyscus*.

Variable code	Predation		Resources				
	Diminished risk	Refuges	Breeding Space	Food	Temporal food and refuges	Permanent	Resting places
			Vegetation Cover (cm)				
VC10	X			X	X		X
VC25	X		X	X	X		X
VC35	X		X	X	X		X
VC50	X		X	X	X		X
VC100	X		X	X	X		X
			Frequency of Herbaceous Plants (cm)*				
FH11	X		X	X	X		X
FH12	X		X	X	X		X
FH13	X		X	X	X		X
FH14	X		X	X	X		X
FH15	X		X	X	X		X
			Frequency of Woody Plants (cm)*				
FW21	X	X	X	X	X	X	X
FW22	X	X	X	X	X	X	X
FW23	X	X	X	X	X	X	X
FW24	X	X	X	X	X	X	X
FW25	X	X	X	X	X	X	X
			Species Vegetation Richness				
VR	X	X	X	X	X	X	X
			Total of Herbaceous Plants				
TH	X		X	X	X		X
			Total of Woody Plants				
TW	X	X	X	X	X	X	X
			Rocks				
RC	X	X	X			X	X
			Organic Matter (litter, twigs, small trunks)				
OM				X	X		
			Bare Soil				
BS					X		
			Coverage of Logs (stumps, fallen trunks)				
CLO	X	X	X			X	X
			Numbers of Burrows				
BW	X	X	X			X	X

* = Frequencies of plant types (FH, FW) involve the same heights as in VC.

Table 2. Normality (**NOR**) tests for 22 variables (**VAR**) of microhabitat, and comparisons[abc] (**COM**) for average values between the dry (**DRY**) and rainy (**RAINS**) seasons, respectively. Variable names in Table 1.

VAR	NOR[a]		COM	VAR	NOR[a]		COM	VAR	NOR[a]		COM
	DRY	RAINS			DRY	RAINS			DRY	RAINS	
BS	0.0001	0.0001	*1.0*[c]	**VC100**	0.002	0.003	0.0001[c]	**TW**	*0.143*	*0.08*	0.0004[b]
CLO	0.0001	0.0001	*0.972*[c]	**VR**	0.006	*0.082*	0.0001[b]	**FW21**	0.0001	0.0001	0.004[c]
OM	0.010	0.034	0.0001[c]	**TH**	0.0001	*0.072*	0.0001[b]	**FW22**	0.0001	0.0001	0.026[c]
RC	0.0001	0.0001	*0.432*[c]	**FH11**	0.015	0.028	*0.658*[c]	**FW23**	0.0001	0.0001	*0.875*[a]
VC10	0.002	0.041	0.0001[c]	**FH12**	0.0001	0.0001	0.001[c]	**FW24**	0.0001	0.0001	*0.378*[c]
VC25	0.009	0.003	0.0001[c]	**FH13**	0.0001	0.0001	0.0001[c]	**FW25**	0.0001	0.001	0.0001[c]
VC35	0.0001	0.002	0.0001[c]	**FH14**	0.0001	0.0001	0.0001[c]	BW	0.0001	0.0001	1
VC50	0.0001	0.019	0.0001[c]	**FH15**	0.0001	0.0001	0.0001[a]				

Parametric: [a]Kolmogorov-Smirnov; [b]Student for two samples; non-parametric: [c]Wilcoxon). The *p*-values in italics do not reject normality ($p \geq 0.05$), or do not indicate significant differences between pluvial seasons.

Table 3. Nearest Neighbor Analysis for both species of *Peromyscus*, it shows the mean distance in which individuals from both *Peromyscus* are segregated. R-value indicates how the observed distribution deviates from random. Clustered points give $R<1$, Poisson patterns give $R\sim1$, while overdispersed points give $R>1$.

	Dry season		Rain season	
	P. difficilis	*P. melanotis*	*P. difficilis*	*P. melanotis*
Points	57	39	58	52
Mean distance	1.40	2.39	1.67	2.09
R	0.42	0.77	0.55	0.64
P value	$1.1263\text{x}10^{-16}$	0.006	$8.6577\text{x}10^{11}$	$8.7708\text{x}10^{7}$
Point pattern	Clustering	Clustering	Clustering	Clustering

Table 4. Principal components used as effect model in the GLMs analysis for both seasons. Red colors represent the variables that have the major eigenfactors to the ordination of the components.

Variables	Dry season			Rainy season		
	PC1	PC2	PC3	PC1	PC2	PC3
VC10	0.713	-0.388	-0.134	0.659	-0.179	-0.374
RC	-0.145	-0.055	-0.110	0.014	0.062	0.034
CLO	0.030	0.118	0.828	-0.153	0.411	-0.583
OM	-0.604	0.303	-0.487	-0.499	-0.122	0.775
BS	0.130	-0.187	0.112	-0.028	0.154	-0.328
VC25	0.415	0.280	0.034	0.658	-0.061	0.237
VC32	0.287	0.184	0.052	0.580	-0.003	-0.126
VC50	0.523	0.107	0.078	0.669	-0.173	-0.030
VC100	0.335	0.408	0.052	0.656	-0.053	0.107
VR	0.762	0.251	-0.269	0.776	0.380	0.058
TH	0.837	-0.430	-0.131	0.874	-0.319	-0.076
TW	0.520	0.684	-0.168	0.615	0.711	0.270
FH11	0.784	-0.394	-0.214	0.678	0.007	-0.228
FH12	0.573	-0.345	0.176	0.548	-0.278	0.256
FH13	0.247	0.073	0.113	0.463	-0.260	0.067
FH14	0.149	-0.186	-0.023	0.580	-0.530	-0.043
FH14	0.080	0.117	-0.236	0.481	-0.267	-0.019
FW21	0.127	0.510	-0.394	0.342	0.603	0.311
FW22	0.015	0.064	-0.105	0.266	0.212	0.416
FW23	0.199	0.256	-0.228	0.196	0.366	-0.241
FW24	0.424	0.359	0.195	0.337	0.165	0.159
FW25	0.515	0.366	0.380	0.494	0.469	0.026
BW	-0.105	0.249	0.557	-0.170	0.332	-0.218

Table 5. Generalized Linear Models constructed with the Principal Components and the frequency of P. *difficils* and *P. melanotis* for both seasons. The partition of resources by both species is observed at both seasons of the year. Different main components within each season explain the frequency of capture of each of the species. Also, the table is related to what type of microhabitat the new variables belong to (M1-M3). The goodness of fit tests are shown; Pearson and Deviance.

				P. difficilis		
				Dry season		
Term	Estimate	Std Error	L-R x^2	*P* value	Pearson	Deviance
Intercept	-0.97	0.15	55.73	0.0001	$x^2 = 155.80$ ($p = 0.0096$)	$x^2 = 123.56$ ($p = 0.3210$)
PC1 = M2	0.11	0.05	5.53	0.0186	AICc = 212.55	
PC3 = M1	0.45	0.06	44.73	0.0001		
				Rainy season		
Term	Estimate	Std Error	L-R x^2	*P* value	Pearson	Deviance
Intercept	-0.40	0.11	14.37	0.0002	$x^2 = 168.56$ ($p = 0.0008$)	$x^2 = 156.43$ ($p = 0.0062$)
PC2 = M3	0.23	0.06	10.92	0.0009	AICc = 286.76	
PC3 = M1	0.26	0.07	10.95	0.0009		
				P. melanotis		
				Dry season		
Term	Estimate	Std Error	L-R x^2	*P* value	Pearson	Deviance
Intercept	-1.21	0.18	74.28	0.0001	$x^2 = 237.65$ ($p = 0.0001$)	$x^2 = 138.70$ ($p = 0.0935$)
PC2 = M3	0.46	0.09	23.34	0.0001	AICc = 204.47	
				Rainy season		
Term	Estimate	Std Error	L-R x^2	*P* value	Pearson	Deviance
Intercept	0.60	0.12	28.15	0.0001	$x^2 = 132.71$ ($p = 0.13$)	$x^2 = 132.72$ ($p = 0.13$)
PC1 = M2	0.10	0.04	4.47	0.0343	AICc = 241.01	

Figure legends

Fig. 1. Sampling plot design. a) Total plot area was 2475 m^2; each intersection (n = 120) was an independent sampling station for capturing mice. An influence area of 2.5 m^2 around each station was constructed for sampling 24 microhabitat environmental variables. b) Close up to the influence area showing the eight transects used for drawing environmental variables; note subdivisions into three subtransects.

Fig. 2. Map of the distribution of the microhabitats (M1 = network, M2 = green, M3 = blue) in the study quadrant for dry (A) and rainfall (B). The bar graph below shows the change in the number of sampling stations between dry and rainy seasons. ** $p = 0.001$

Fig. 3. Box-plots are showing the seasonal heterogeneity of the 23 variables sampled in the study plot between dry and rainy seasons. Overall, vegetation variables show an increase in the rainy season, while the organic matter (OM) decrease. Structural elements as logs on the ground do not shot differentiation between seasons. Some variables were not present in high quantities along the study plot. Therefore we were unable to build the box-plot. The red cross represents the mean of each variable.

Fig. 4. Spatial analysis with Kernel density points showing capture frequencies for *P. difficilis* at dry (a) and rainy (b) seasons, and for *P. melanotis* at dry (c) dry and rainy (d). Dots depict actual capture points, while hot spots color indicates higher density.

Fig. 5. Correspondence analysis from contingency tables of frequency capture data for each deermouse (*P. difficilis* and *P. melanotis*) in each microhabitat (M1-3), during the dry (a) and rainy (b) seasons, respectively. Axis c1 and c2 indicate the coordinates resulted from the ordination of each variable from the analysis. Figure c shows the plots for the GLMs models, the response variable for each graph are the predicted values of the model to that principal component (the model effect). All of the PCs fitted in the model

show a positive relationship, indicating that the probability of capture frequency of the individuals of two mice, increases with the presence of that variables. Therefore, the figure also shows in the “X” axis in parenthesis the variables with the higher loading scores in the ordination of this PCs.

Fig. 6. Ripley's bivariate K Analysis for interactions between the two *Peromyscus*. (a) Repulsion pattern between both species in all analyzed distances during the dry season. (b) Attraction from 6 - 12 m, and repulsion at 5, 11, and 14 m during the rainy season. Black solid line represent the Ripleys K bivariate pattern; red dashed lines represent the 95% CI; blue solid line shows the null hypothesis.

Fig. 1

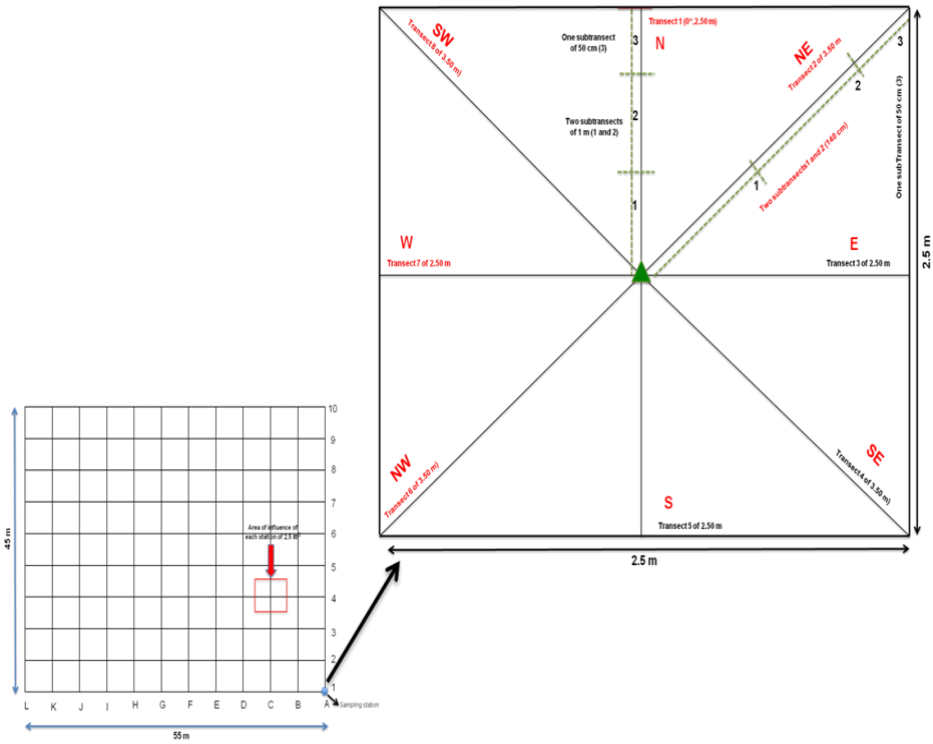

SW
Transect 8 of 3.50 m)
One subtransect of 50 cm (3)
Transect 1 (0°, 2.50 m)
N
NE
Transect 2 of 3.50 m
Two subtransects of 1 m (1 and 2)
Two subtransects 1 and 2 (140 cm)
One sub Transect of 50 cm (3)
W
Transect 7 of 2.50 m
E
Transect 3 of 2.50 m
2.5 m
NW
Transect 6 of 3.50 m)
S
Transect 5 of 2.50 m
SE
Transect 4 of 3.50 m)
2.5 m
Area of influence of each station of 2.5 m²
45 m
55 m
L K J I H G F E D C B A
Sampling station

Fig. 2

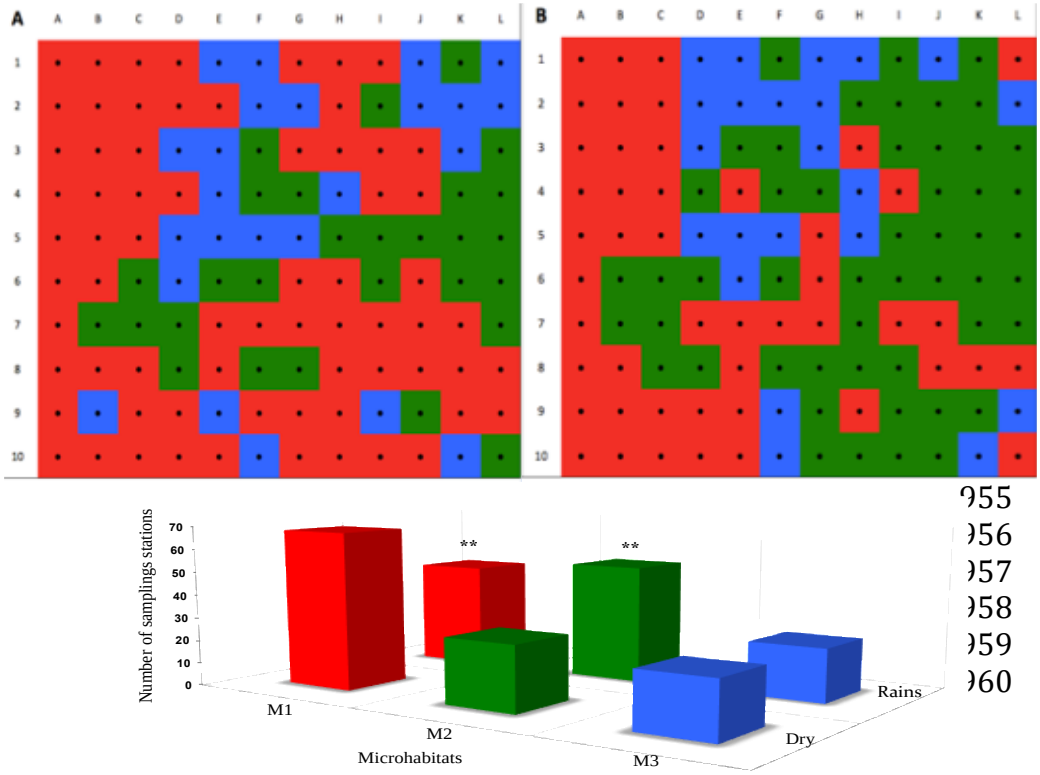

A
B
Number of samplings stations
70
60
50
40
30
20
10
0
**
**
M1
M2
M3
Microhabitats
Rains
Dry

Fig. 3

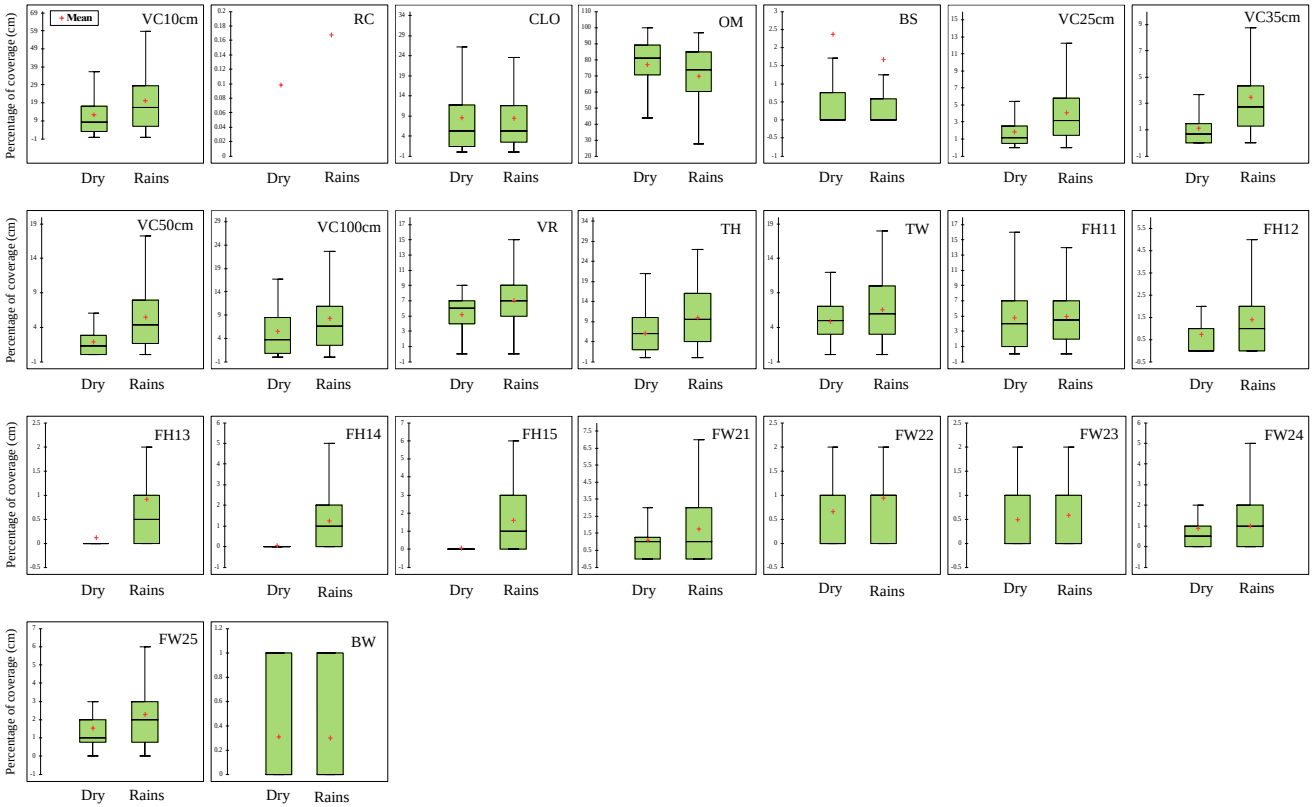

Mean
VC10cm
RC
CLO
OM
BS
VC25cm
VC35cm
VC50cm
VC100cm
VR
TH
TW
FH11
FH12
FH13
FH14
FH15
FW21
FW22
FW23
FW24
FW25
BW
Percentage of coverage (cm)
Dry
Rains

Fig. 4

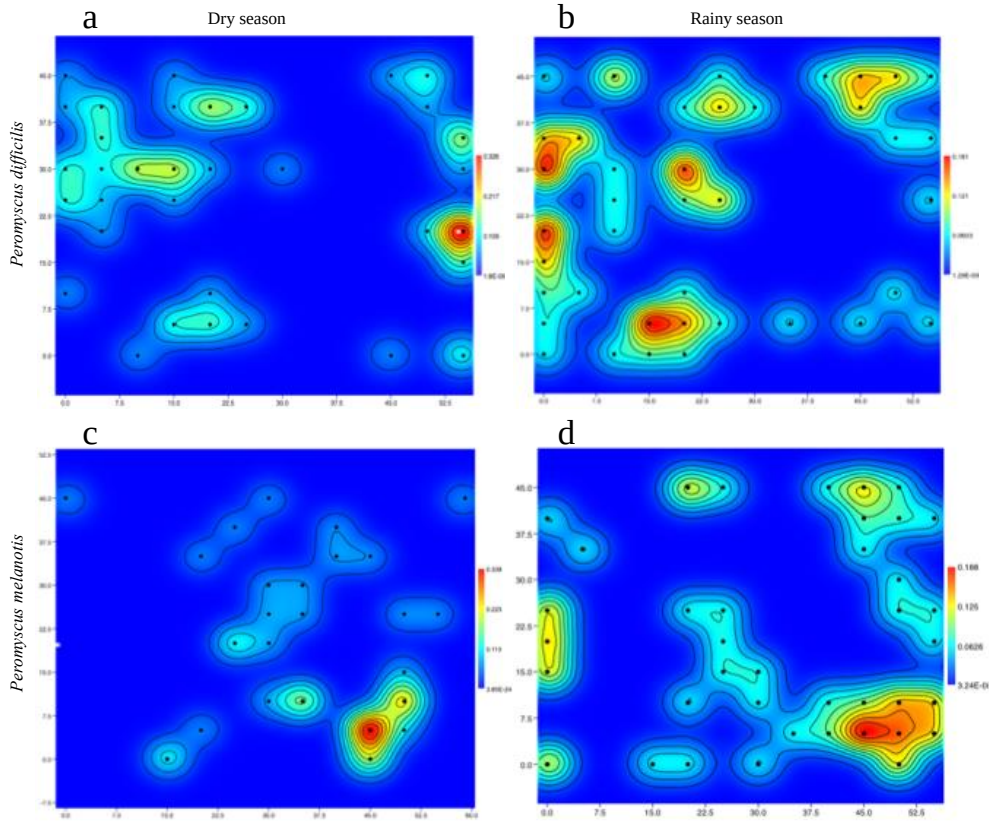
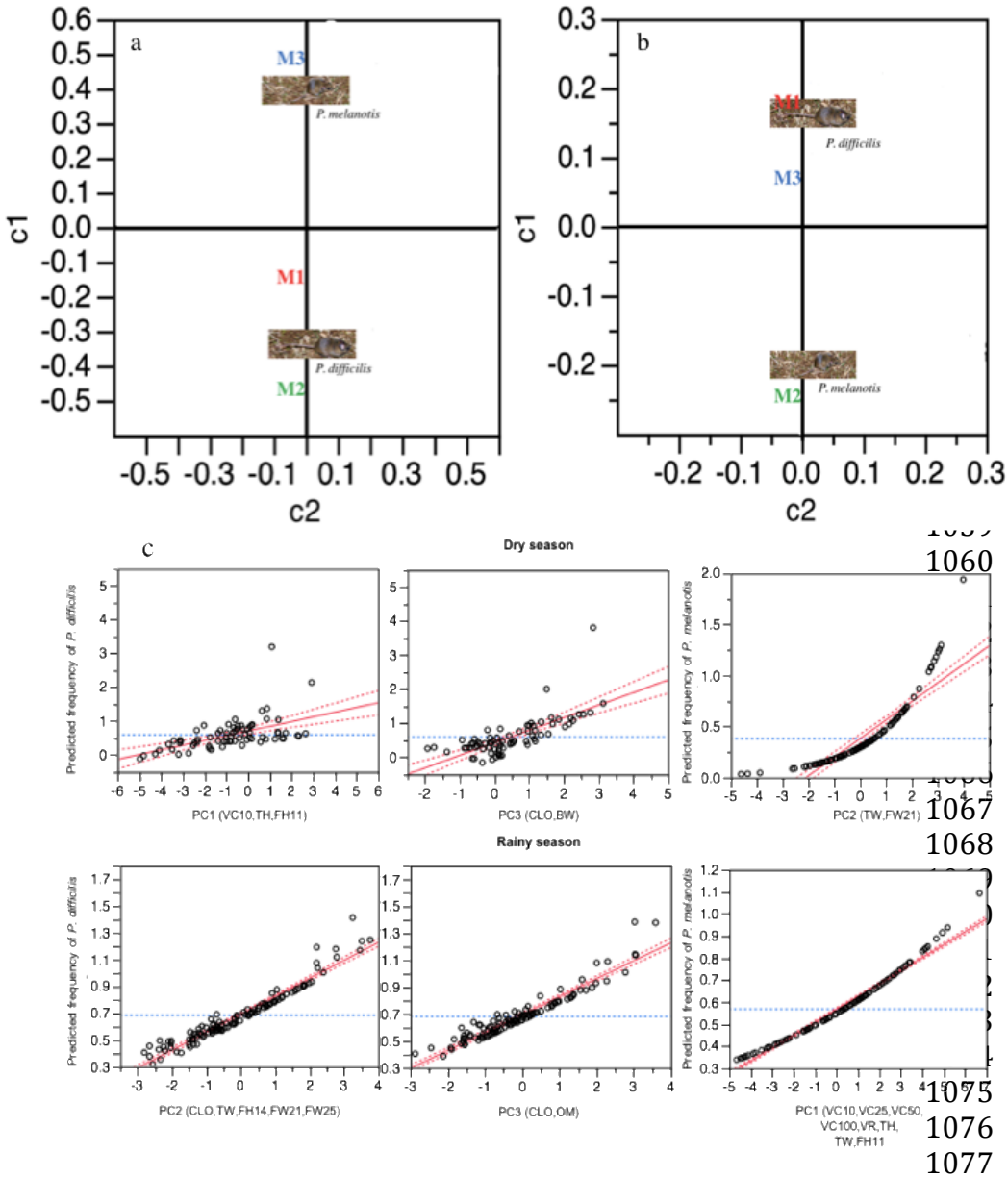

a
Dry season
b
Rainy season
c
d
Peromyscus difficilis
Peromyscus melanotis

Fig. 5


a
M3
P. melanotis
M1
P. difficilis
M2
c1
c2
b
M1
P. difficilis
M3
M2
P. melanotis
c
Dry season
Predicted frequency of P. difficilis
PC1 (VC10,TH,FH11)
PC3 (CLO,BW)
Predicted frequency of P. melanotis
PC2 (TW,FW21)
Rainy season
PC2 (CLO,TW,FH14,FW21,FW25)
PC3 (CLO,OM)
PC1 (VC10,VC25,VC50, VC100,VR,TH, TW,FH11

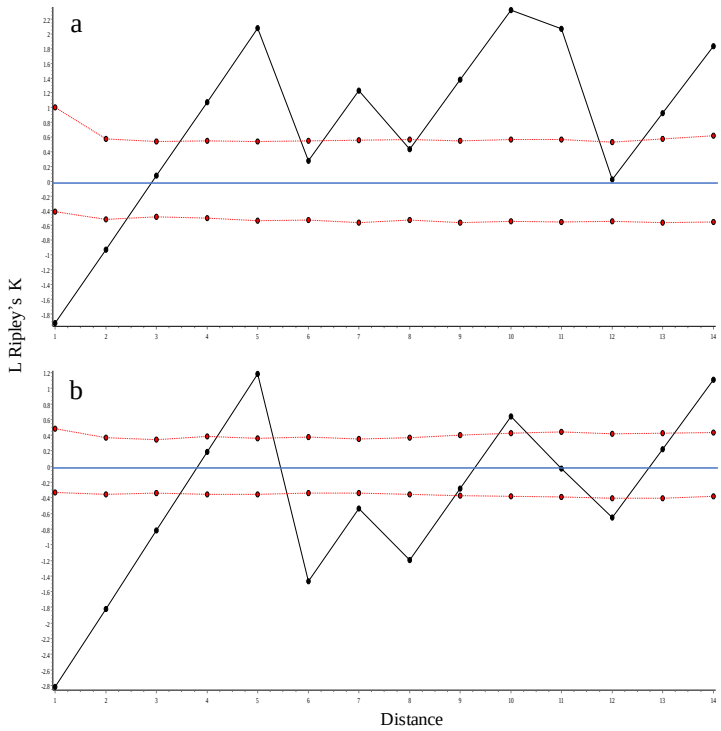



Fig. 6